

STRUCTURE OF SOIL FOOD WEB IN SMALLHOLDER COCOA PLANTATION, SOUTH KONAWE DISTRICT, SOUTHEAST SULAWESI, INDONESIA

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ABSTRACT

An understanding of the structure of the soil food web is critical in determining the practices of soil fertility management based on the biological processes in tropical agricultural regions. The objectives of the study were to assess the variation in trophic level biomass and to analyze the dynamics of the energy channels on the increasing age of cocoa plantation. The characteristics of soil food web structure in smallholder cocoa plantation aged 4, 5, 7, 10, and 16 years were analyzed. The results showed that only biomass at the third trophic level increased with plantation age, but not for the biomass at the lower trophic levels. Biomass in all energy channels did not increased as well along with plantation age. We concluded that variation in the soil food web structure was more influenced by biotic factors of macro-arthropods group, such as facilitation, recolonization capabilities and accessibility in the soil habitat of smallholder cocoa plantation.

Keyword: biomass, biotic, energy channel, trophic level

INTRODUCTION

The process of decomposition and nitrogen mineralization involves trophic interaction between soil fauna and microbes in soil food web (Schimel and Bennett, 2004; Osler and Sommerkorn, 2007). Structures of soil food web are playing an important role in explaining the effect of changes in the composition and diversity of species on the pathway in decomposition and nitrogen mineralization by soil biota community

(Berg *et al.*, 2001; Holtkamp *et al.*, 2011). Soil organic matter and root are the primary energy source for microbes and soil fauna (Moore *et al.*, 2004; Petchey *et al.*, 2010). Fraction of soil organic matter is labile organic fraction that can be accessed by bacteria, fungi as well as saprophagous macro-arthropods, and recalcitrant organic fraction which is generally more accessible by fungi and saprophagous macro-arthropods (Hunt *et al.*, 1987; Coleman, 2008).

Energy and nutrients from soil organic matter supplied occupying at the higher trophic level can go through the channels of bacterial, fungal, and saprophagous macro-arthropods in soil food web community (Susilo *et al.*, 2004; Moore *et al.*, 2005; Bardgett and Wardle, 2010). The process of nutrients in bacterial biomass flowing into bacterivore up to the top predators is known as bacterial energy channel, while the nutrients from fungal biomass flowing into the fungivora up to the top predators is known as fungal energy channel, and nutrients from root biomass flowed by nematodes and root-feeding insects up to the top predator is known as root energy channels (Moore and Hunt, 1988; Moore *et al.*, 1988; Berg *et al.*, 2001). Moreover, nutrients flowing from saprophagous macro-arthropods biomass to their consumer and finally up to the top predator could be referred as saprophagous macro-arthropods energy channel in soil food web community.

Development stages of agricultural practices and succesional vegetation affect energy channels in the soil food web. Generally, the factors causing changes in the energy flow will alter the quality and availability of organic substrates as a source of energy and nutrients for microbes and soil fauna (Loranger-Merciris *et*

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al., 2008). Didden *et al.* (1994) found the biomass of fungivore soil fauna more dominant than bacterivore soil fauna biomass in agricultural systems minimized in soil tillage, use of inorganic fertilizers, and biocides. The biomass ratio of fungi to bacteria, biomass ratio of fungal energy channels to bacterial energy channels, and biomass ratio of bacterivore to fungivore in the former agricultural land was lower than that of the natural forest land (Holtkamp *et al.*, 2008). Root biomass does not only contribute to soil organic matter content (Hertel *et al.*, 2009), but it also serves as carbon and nutrient source for soil fauna. Biomass of root-feeding nematodes tend to decrease with age of vegetation (Holtkamp *et al.*, 2008), for it is allegedly associated with increased concentrations of defense compounds (i.e. terpenoids) in root tissues, so it is not easily accessed by groups of nematodes and insects (Bonkowski *et al.*, 2009). The quality of root tissues not only affects the abundance of root-feeding nematodes (Marhaning *et al.*, 2009; Viketoft *et al.* 2009), but also the abundance of root-feeding insects and saprophagous macroarthropods (Doblas - Miranda, 2009).

An understanding of the dynamics of the energy channels in the soil food web is critical in determining the regulation of agricultural soil fertility management practices based on biological processes in tropical environment (Swift, 1997). However, studies related to the dynamics of the soil food web structure in the tropical agroecosystem, especially in smallholder cocoa plantation are still neglected. Indonesia was in the world's third rank, and it was in the first rank in Asia-Pacific as cocoa bean producer (ICCO, 2010). In this region, approximately 94 % of the total area of cocoa plantations was managed by small farmers (Directorate General of Estate, Agricultural Ministry RI, 2012). By some researchers was proposed a small-holder cocoa plantation as management land system suitable for the soil biodiversity conservation (Delabie *et al.*, 2007; Moco *et al.*, 2009).

The studies related to the dynamic of soil biota community structures was still focused on composition and diversity of soil fauna community from different managemen system and different age of cocoa plantation (Moco *et al.*, 2009; Kilowasid *et al.*, 2012; Kilowasid *et al.*, 2013). Meanwhile, up to now the study how the

pattern changes in the structures of soil food web with age of small-holder cocoa plantation is still rare. The objectives of the study are to assess the variation in biomass of trophic level and to analyze the dynamics of the energy channels in the soil food web among ages of small-holder cocoa plantation.

MATERIALS AND METHODS

Study Site

The study was conducted in Konda and Mowila sub-District, South Konawe District, South East Sulawesi in smallholder cocoa plantation aged 4 years (040 08' 33.2"S; 122 031' 01.7"E), 5 years (040 08' 50.5"S; 122 030' 41.04"E), 7 years (040 08' 44.4"S; 122 030' 47.7"E), 10 years (040 08' 34.4"S; 122 031' 40.5"E), and 16 years (040 07' 04.9"S; 122 015' 02.8"E). The average of rainfall was 175.58 mm month⁻¹ and air temperature was 26.74°C. The topography of the research area was categorized as flat with the slope class of 0-3%. Soil type was categorized as a sub-group Dystrudept Typical, coarse clay, Isohypertermic. The location description of every plantation was described in Kilowasid *et al.* (2012) and the soil characteristics in the Kilowasid *et al.* (2013).

Sample Collection of Soil Organic Fraction, Root and Soil Organisms

Organic fraction of the soil, roots, microbes and soil fauna were put on a square of 2500 m² (50 mx 50 m) on each cocoa plantation. All samples were taken from each site with 15 cm in soil depth using stainless steel cylinders. The samples for analysis of soil organic fractions were collected on August 15, 2010 using soil cores with a 7.4 cm-in-diameter cylinder on each corner of the square of each place. Samples of active roots, microbes, protozoa, nematodes, acari, collembola, enchytraeids and soil macrofauna were collected five times over a period of a year on August 1, 2009, 21 November 2009, January 26, 2010, 22 April 2010, and June 13, 2010. Each time the sampling was constructed of four sub - squares (each sub - sized 0.5mx 0.5m square) were placed between the cocoa crop in the size of 3m x 3m, and the distance between the sub - squares to 10 m in each square at each place (for more details of the sampling design see Kilowasid *et al.*, 2012 and Kilowasid *et al.*, 2013). At every time point in

each sub-sample was taken for analysis of soil microbes and protozoa using a stainless steel cylinder of 7.4 cm in inner diameter. Soil sample for analysis of microbial analysis, protozoa, enchytraeid, nematodes and soil mesofauna was put in different zipper packs, and each was placed in a cool box and transported to the laboratory.

Determination of Soil Organic Fraction and Root Biomass

Fraction of labile soil organic matter and recalcitrant were extracted following the acid hydrolysis two-step procedure with H₂SO₄ as solvent extraction (Rovira and Vallejo, 2002; Rovira and Vallejo, 2007; Belay-Tedla *et al.*, 2009). Separation of active roots from the soil following the procedure is described in Kilowasid *et al.* (2013). Fresh root was dried at a temperature of 70°C for 48 hours (Munoz and Beer, 2001). After the dry weight was weighed, then the root was smoothed using a blender to analyze the C root tissue.

Analysis of Soil Organism Biomass

The biomass of each soil organism group was expressed in kg C/ha/15 cm in soil depth. The number of bacteria in the soil samples was estimated, following the procedure by Trolldenier (1996). Cell number of soil bacteria stained with acridine orange on a microscope slide was counted under epifluorescence microscope which was magnified 500 times, and as many as 20 fields of view were obtained. The number of bacteria was then converted into biovolume using a factor of 0.5236 $\mu\text{m}^3 \text{ cell}^{-1}$ (Klein and Paschke, 2000). The biovolume of bacteria was changed into bacterial biomass using a conversion factor ($3.20 \times 10^{-13} \text{ g C } \mu\text{m}^{-3}$) (Bakken and Olsen 1985). Soil fungal biomass was estimated with an approach of fluorescein diacetate hydrolysis method, following the procedures explained by Green *et al.* (2006). Fluorescein content in the soil was converted to fungal biomass with a regression model reported by Gaspar *et al.* (2001), and 40% carbon content of fungal biomass (van Veen and Paul, 1979).

The number of active flagellates was estimated from 15 μl soil suspension (1:5) in a hemocytometer chamber and counted under the objective lens light microscope at a magnification of 400 times, while the number of

active amoebae in soil suspensions (1:10) in a petri dish was counted under an inverted phase contrast microscope magnified 200 times, following the procedure of Adl *et al.* (2008). Individuals of flagellates were converted to biovolume with a conversion factors of $50 \mu\text{m}^3$ per flagellates (Stout and Heal, 1967). For amoeba, the $400 \mu\text{m}^3$ convention factor per amoeba was used (Ekelund *et al.*, 2001), and biomass of flagellates and amoeba were calculated with this assumption: $1.1 \times 10^{-13} \text{ g C } \mu\text{m}^{-3}$ (Adl *et al.*, 2008).

Free nematodes were extracted from soil using a modified technique of Funnel Baerman (Kilowasid *et al.*, 2013). Nematode individuals were counted under a dissecting microscope and a minimum of 100 individuals were identified up to family level under a light microscope, magnified 400 times. Every family was allocated to the feeding type grouping as in Yeates *et al.* (1993). Every nematode was converted to wet weight using a conversion factor value by Ferris (2010). The wet weight was converted to dry weight using the ratio dry weight: wet weight was 0.21 (Yeates, 1979) and 50% carbon content of dry weight (Beare *et al.*, 1992).

Soil meso-fauna including Acari (mites), Collembola and adult Diptera were extracted from soil using a Berleses Tullgren technique at 38- 40°C room temperature for five days. Each soil meso-fauna was preserved in 70% alcohol and counted under a dissecting microscope. Acari, Collembola, and Diptera, which had been cleaned and mounted, were identified up to morphospecies level. Individuals of Acari were converted to biomass using a conversion factor of carbon content of dry weight from each group. Oribatida was $2.39 \mu\text{g C individual}^{-1}$, Mesostigmata $3.47 \mu\text{g C individual}^{-1}$, Prostigmata $0.45 \mu\text{g C individual}^{-1}$ (Beare *et al.*, 1992) and Astigmata $0.26 \mu\text{g C individual}^{-1}$ (Persson and Lohm, 1977; Berg *et al.*, 1998). Diptera and Collembola biomass having been preserved in 70% alcohol were estimated using the relationship between dry weight and body length based on the formula from Ganihar (1997) and 50% carbon content of dry weight (Bezemer *et al.* 2010).

Enchytraeid was extracted using a modified Baerman funnel extractor under room temperature of 38 - 40°C for five days, and the individuals were counted under a dissecting microscope. Dry weight of enchytraeid was

estimated using an average of 0.031 mg dry weight per individual (Persson and Lohm, 1977) and 50% carbon content of dry weight (Bezemer *et al.*, 2010).

Soil macrofauna from soil was removed using a hand sorting techniques, and the specimens preserved in alcohol 70% were identified up to morphospecies. Dry weight of each taxon of macrofauna was estimated using allometric equation between dry weight and body length of specimens that had been preserved in 70% alcohol (Collins, 1991; Ganihar 1997; Sabo *et al.* 2002; Gruner 2003; Brady and Noske, 2006; Höfer and Ott., 2009) and carbon content assumed 50% of dry weight for each taxa (Bezemer *et al.* 2010).

Diagram of Soil Food Web

The diagram of the soil food web was constructed by grouping soil organism taxa based on the similarity in their prey, predator, growth rate and survival rate (Moore *et al.*, 1988; Moore, 1994; Sugihara *et al.*, 1997). Construction of the soil food web in this study was developed from a generic soil food web for tropical agricultural proposed by Susilo *et al.* (2004). The generic soil food web model combined with the latest knowledge about the feeding habit of functional groups in soil food webs from a number of ecosystem types and climates was previously described by some authors (i.e. Berg *et al.*, 2001; Schröter *et al.*, 2003; Holtkamp *et al.*, 2008; Bezemer *et al.*, 2010). The soil food webs for smallholder cocoa plantation is described in the following diagram (for more details see Kilowasid, 2012)

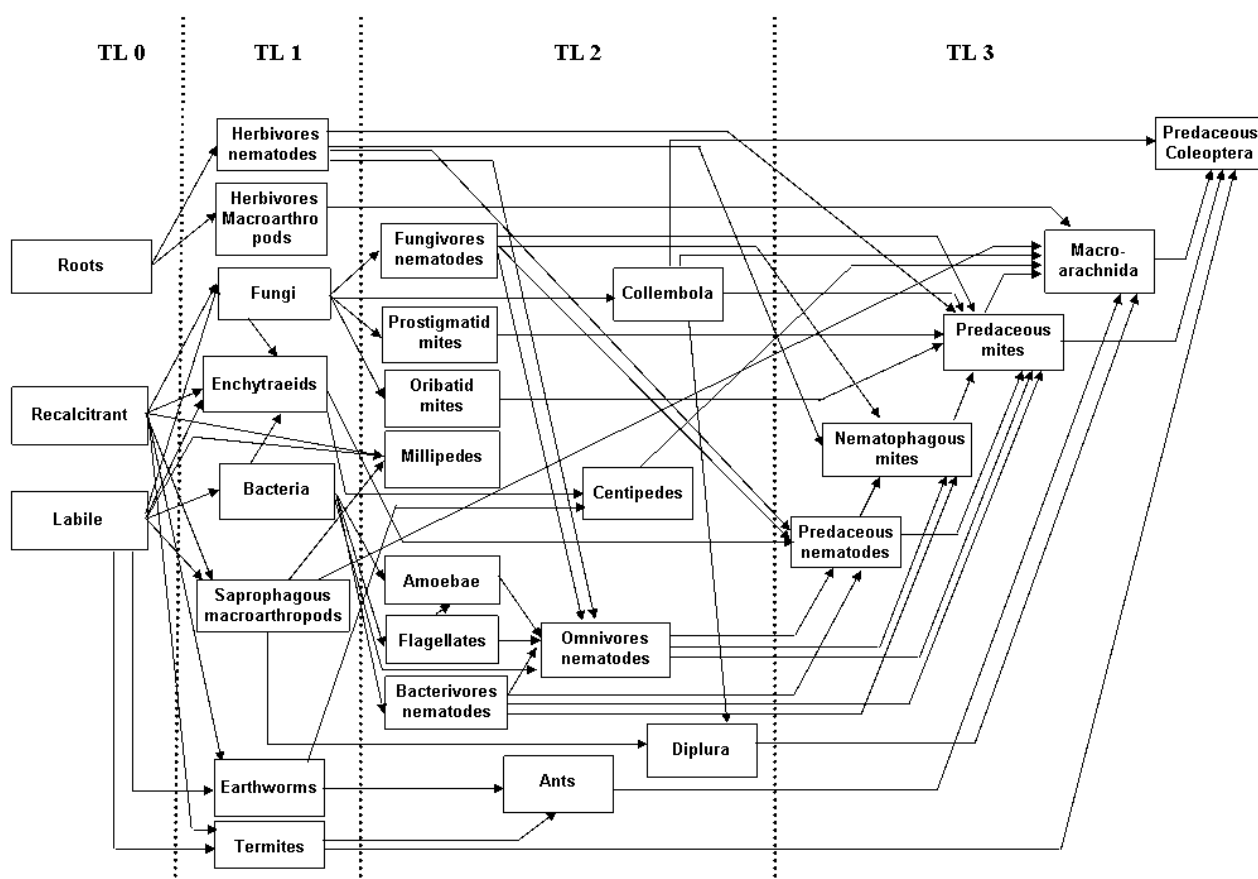


Figure 1. Diagram of soil food web in smallholder cocoa plantation. Box indicates trophic group, an arrow indicates direct of energy flow. TL shows trophic level

Analysis of Characteristics of Soil Food Web Structure

Trophic level

Labile organic fraction, organic fraction recalcitrant and the root were the primary energy sources of functional groups in soil food web and set occupied at the basal trophic and referred as zero trophic levels (Rooney *et al.*, 2006; Holtkamp *et al.*, 2008). Trophic position of each predator is determined using the following formula (Williams and Martinez, 2004; Rooney *et al.*, 2006):

$$TL_j = 1 + \sum_{i=1}^n p_{ij} \times TL_i$$

where TL_j is the trophic level of the higher order predator trophic position, TL_i is trophic level of the prey, n is the number of prey consumed by the predator, p_{ij} is the dependent feeding preference of predator j on prey i .

The dependent feeding preference of predator j on prey i (p_{ij}) was calculated with formula by Hunt *et al.* (1987):

$$p_{ij} = \frac{w_{ij} B_i}{\sum_{i=1}^n w_{ij} B_i}$$

Where, w_{ij} is a weighing factor, n is the index for summation over all (n) trophic groups on which j preyed, B_i is the biomass of prey i .

Generally, feeding preferences of top predators on certain prey types in the soil food web modeling used dietary data on estimated percentage of each functional group (flagellates, amoebae, nematodes, acari, Collembola, enchytraeids and earthworms) following de Ruiter *et al.* (1994) and Didden *et al.* (1994). Meanwhile, feeding preference data for other soil macro-invertebrates for the soil food web modeling has not been published (Holtkamp *et al.*, 2011). To overcome the limitation of the data availability related to dietary percentage for macro-invertebrates functional groups to determine the feeding preference weight of a predator on prey particular types, the weighting factor (w_{ij}) used was 1, which is based on the consideration that consumption depends on the relative abundance of prey predator (Berg *et al.*, 2001). Every trophic level biomass was calculated by summing the biomass from each

trophic group within the respective trophic levels (Holtkamp *et al.* 2008).

Energy Channel

Energy channels of root, bacteria, fungi, and saprophagous micro-arthropods were quantified by summing the biomass of all trophic groups that obtained energy from each channel. A trophic group gained more energy from the primary sources contributed to more than one channel of energy. The roots were assumed to contribute over the energy channels through the root-eating nematodes and herbivorous macro-arthropod. Labile organic fraction contributed fully to channel the energy that flows through bacteria, saprophagous macro-arthropods, enchytraeidae, and milipedes. Labile and recalcitrant organic fraction contributed equally to the energy channels in fungi, saprophagous macro-arthropods, termites, earthworms and milipedes. Contributions of another group to each energy channel were calculated using the feeding preference rate. Before the feeding preference rate was calculated, biomass group at every trophic level was standardized with the way each trophic group of biomass was divided by the total biomass from all groups which constituted the soil food web community multiplied by 100. Based on the standardized biomass, later the contribution of each group in the energy channel was calculated with the procedure from Holtkamp *et al.* (2008).

Statistical Analysis

To detect differences of biomass in trophic level and energy channels from the soil food web among different ages of cocoa plantations, univariate analysis of variance with least significant differences (LSD) post hoc test was applied. The assumption of normality was tested using the Shapiro-Wilk and the assumption of homogeneity of variance between groups was tested with Levene's test. To detect the changing trend of every trophic level biomass and energy channel biomass along the age of cocoa plantation, linear regression analysis was employed.

RESULTS AND DISCUSSION

Biomass of trophic level

Fraction of soil organic and roots were placed at the trophic level 0 in diagram of soil

food web (Figure 1). In chronosequence approach it was often hypothesized that biomass at trophic level 0 of soil food web tended to increase linearly with age of vegetation (Holtkamp *et al.*, 2008). In this study, biomass at the trophic level 0 did not show a linear increase with age of cocoa plantation ($p = 0.073$; $R^2 = 0.168$). The content of each soil organic fraction in all cocoa plantations was relatively the same (Table 1). These results were similar to findings by Smiley and Kroschel (2009), where the soil organic carbon content did not change significantly along the age of smallholder cocoa plantation. Biomass at the trophic level 0 was composed the fraction of soil organic matter plus root biomass. Biomass at the trophic level 0 in cocoa plantation aged 16 years was lowest ($LSD > 0.05$) compared with that of 5 years, but the differences were not significant compared to the biomass in other cocoa plantation (Figure 2A). Biomass of root was significantly different between the ages of cocoa plantations (Table 2). Biomass of root in the plantation aged 4 to 5 years increased significantly ($p < 0.05$), and active root biomass after the cocoa plantation aged 5 years tended to reduce with age of the cocoa plantation. This pattern of reduction in root biomass is similar to the findings of Smiley and Kroschel (2008) on the pattern of changing biomass of cocoa root in Napu, Central Sulawesi. Although biomass of root between cocoa plantations differed significantly, but its influence could not change the contribution effect of the soil organic fraction to biomass at the trophic level 0 with age of the cocoa plantation.

Biomass at the trophic level 1 consisted biomass of saprophagous macro-arthropods, herbivorous macro-arthropods, termites, earthworms, Enchytraeidae, bacteria, fungi and root-feeding nematodes (Figure 1). Biomass at the trophic level 1 (Figure 2B) did not show a significant increase ($p = 0.925$; $R^2 = 0.001$). Biomass with trophic level 2 was composed of centipedes, milipedes, Diplura, ants, flagellates, amoeba, prostigmatid mites, oribatid mites, Collembola, omnivorous, bacterivorous, and fungivorous nematodes (Figure 1) also showed no significant increase with age of cocoa plantation ($p = 0.120$; $R^2 = 0.129$). Biomass at the trophic level 2 on plantation aged 5 years was the lowest, and on the plantation aged 10 years was the highest (Figure 2C). Table 2

shows that the biomass of centipedes, milipedes and diplura on cocoa plantation aged 5 years was the lowest, while biomass of centipedes and Diplura at the plantation aged 10 years and milipedes at the plantation aged 16 years was the highest. Biomass of ants, all groups of micro-arthropods and flagellates between age of cocoa plantation were not significantly different. Biomass of amoeba in cocoa plantation aged 5 years was the highest and in the aged 16 years it was the lowest. Biomass of omnivorous, bacterivorous and fungivorous nematodes at the plantation aged 4 years was the highest. Biomass of bacterivorous and fungivorous nematode in cocoa plantation aged 5 years and omnivorous nematode in cocoa plantation aged 16 years was the lowest.

Biomass at trophic level 3 consisted of biomass from predacious Coleoptera, macro-Arachnida, Acari predaceous, Acari nematofagus (uropodina) and pretadecous nematode (Figure 1) showing a tendency to increase linearly with age of cacao plantation ($p = 0.437$; $R^2 = 0.034$). Biomass at the trophic level 3 on cocoa plantation aged 4 years was the lowest, while the biomass at the trophic level 3 on cocoa plantation aged 16 years was the highest (Figure 2D). It is presented in Table 2 that biomass of macro-arachnids and predaceous coleoptera in cacao plantation aged 5 years was the lowest, while biomass of predaceous coleoptera and macro-arachnids in plantation aged 16 years was the highest. Biomass of predaceous acari in cocoa plantation aged 5 years was higher than biomass of predaceous acari in other plantations, while biomass of nematophagous acari in all cocoa plantations was similar. Biomass of predaceous nematode in cocoa plantation aged 5 years was the highest, and its biomass in cocoa plantation aged 4 years was the lowest. Biomass of predaceous nematodes in cocoa plantation aged 4 and 5 years were not significantly different from those of cocoa plantation aged 7, 10, and 16 years. These facts showed that the group of saprophagous, herbivorous or omnivorous macro-arthropods influenced biomass of other functional groups in soil food web communities, so that in this study it was showed that the biomass of trophic levels had no tendency to decline or increase linearly with age of cocoa plantation. Thus, the results achieved in this study are linear with what was reported by

Susilo *et al.* (2004) that the prediction of an increase or decrease in abundance of functional groups in the soil biota community should be seen as a "random walk" because the accessibility and the recolonisation from some taxa of macro-arthropods, such as ants, Coleoptera, Diptera, Centipedes, and Dermaptera (Wallwork, 1970) are playing an important role in controlling the abundance within trophic levels (Hubbell, 2001).

Biomass of Energy Channel

The biomass of root energy channels did not show a linear increase with age of cocoa plantation ($R^2 = 0.014$ $p = 0.624$). A similar pattern was also shown by the biomass in fungal energy channels ($R^2 = 0.120$ $p = 0.134$), bacterial energy channel ($R^2 = 0.006$ $p = 0.747$), and saprophagous macro-arthropod energy channels ($R^2 = 0.130$ $p = 0.119$).

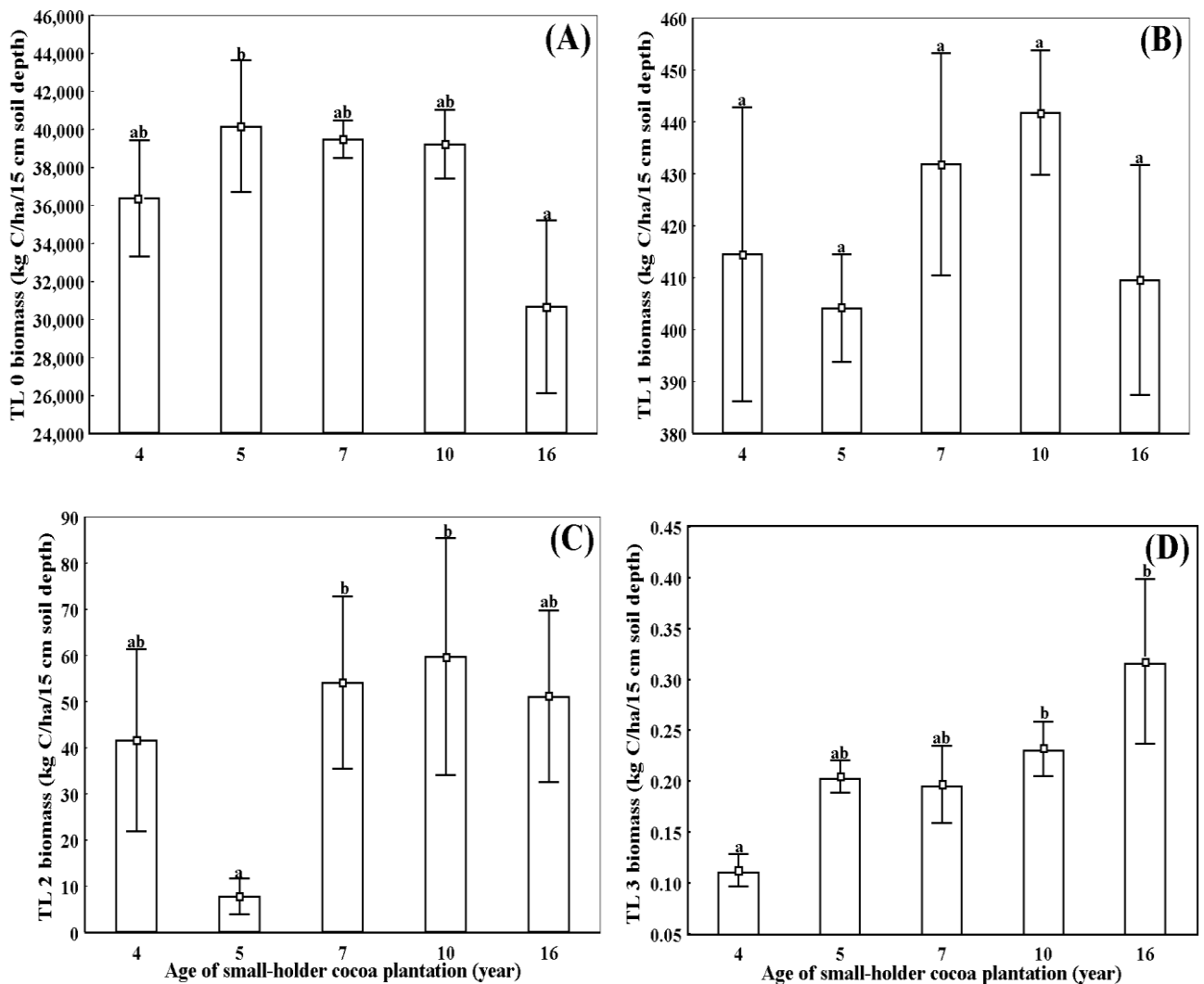


Figure 2. Biomass from: (A) trophic level 0 (TL 0); (B) trophic level 1 (TL 1); (C) trophic level 2 (TL 2); (D) trophic level 3 (TL 3) in soil food web at small-holder cocoa plantation aged 4, 5, 7, 10, and 16 years. Different letters above the bars indicate significant difference between age of small-holder cocoa plantation at the $p < 0.05$ level.

Table 1. Biomass of functional group in different age of smallholder cocoa plantation (kg C/ha/ 15 cm, soil depth)

Functional Group	Age of smallholder cocoa plantation (years)				
	4	5	7	10	16
Labile organic fraction	23051.14±859.5a	21686.85±1639.01a	22326.86±1346.47a	24082.16±4473.27a	20976.41±3998.72a
Recalcitrant organic fraction	12559.28±2486.99a	16368.41±4016.37a	15192.11±2383.52a	13392.26±4774.42a	8137.99±696.77a
Root	771.34±59.91a	2115.38±245.45b	1974.31±253.15b	1738.86±214.94b	1571.13±255.44b
Microbe:					
Bacteria	8.79±1.32a	9.08±0.56a	8.23±0.99a	8.57±0.88a	7.12±0.66a
Fungi	395.65±23.49a	393.14±9.69a	421.98±20.03a	423.14±9.93a	395.58±19.62a
Protozoa:					
Flagellata	0.25±0.06a	0.30±0.09a	0.32±0.05a	0.26±0.06a	0.35±0.05a
Amoebae	0.16±0.02ab	0.23±0.05b	0.21±0.04ab	0.25±0.03b	0.13±0.01a
Microarthropods:					
Collembola	2.80±1.88a	6.36±2.28a	4.49±1.55a	4.02±1.32a	2.01±0.94a
Predaceous mites	0.0212±0.0152a	0.0542±0.0144b	0.0123±0.0069a	0.0212±0.0079a	0.0191±0.0080a
Nematophagous mites	0.0088±0.0088a	0.0088±0.0088a	0.0177±0.0125a	0.0133±0.0085a	0.0044±0.0044a
Oribatid mites	0.0091±0.0058a	0.0061±0.0061a	0.0122±0.0050a	0.0122±0.0050a	0.0061±0.0035a
Prostigmatid mites	0.0034±0.0011a	0.0046±0.0019a	0.0017±0.0017a	0.0057±0.0011a	0.0046±0.0016a
Nematodes:					
Predators	0.4716±0.0580a	0.9598±0.0695b	0.7227±0.1101ab	0.7524±0.0832ab	0.7517±0.0564ab
Omnivores	0.4075±0.0751b	0.0013±0.0003ab	0.0089±0.0028b	0.0012±0.0001ab	0.0000±0.0000a
Bakterivores	0.2543±0.0231b	0.0775±0.0073a	0.2144±0.0314ab	0.1879±0.0103ab	0.1428±0.0151ab
Fungivores	0.0121±0.0025c	0.0000±0.0000a	0.0043±0.0009bc	0.0006±0.0000abc	0.0002±0.0000ab
Herbivores	0.1978±0.0125ab	0.3444±0.0762b	0.0543±0.0087ab	0.3749±0.0773b	0.0142±0.0027a
Macroarthropods:					
Macro-Arachnida	0.012±0.003a	0.00±0.00a	0.046±0.018ab	0.077±0.037ab	0.163±0.083b
Centipedes	1.68±1.68a	4.14±2.41a	25.31±9.40b	46.37±23.89b	3.44±3.05a
Predaceous Coleoptera	1.67±1.14ab	0.13±0.06a	0.92±0.80ab	1.87±1.57ab	14.68±12.99b
Saprophagous	0.28±0.09a	0.17±0.08a	0.64±0.25ab	0.91±0.19b	0.62±0.17ab
Milipedes	0.00±0.00a	0.00±0.00a	7.92±6.80ab	3.67±2.24ab	10.20±5.67b
Diplura	0.335±0.335a	0.00±0.00a	0.821±0.314ab	3.617±1.222b	1.210±1.004ab
Herbivores	9.03±6.00a	1.40±1.38a	0.40±0.37a	7.59±5.39a	5.84±3.00a
Ants	37.39±20.45a	2.96±1.82a	18.56±11.32a	3.65±1.92a	21.08±15.45a
Termites	0.00±0.00a	0.00±0.00a	0.00±0.00a	0.083±0.050a	0.004±0.004a

Table 1 (Continued)

Functional Group	Age of smallholder cocoa plantation (years)				
	4	5	7	10	16
Oligochaeta:					
Earthworms	0.123±0.036a	0.062±0.033a	0.205±0.054abc	0.375±0.133c	0.095±0.026ab
Enchytraeids	0.614±0.217ab	0.242±0.108a	0.413±0.137ab	1.103±0.538b	0.271±0.142ab

Remarks: Numbers followed by different letter within a column indicate significant difference in functional group biomass (n = 20, mean±standard error) between the cocoa plantations at p < 0.05 level

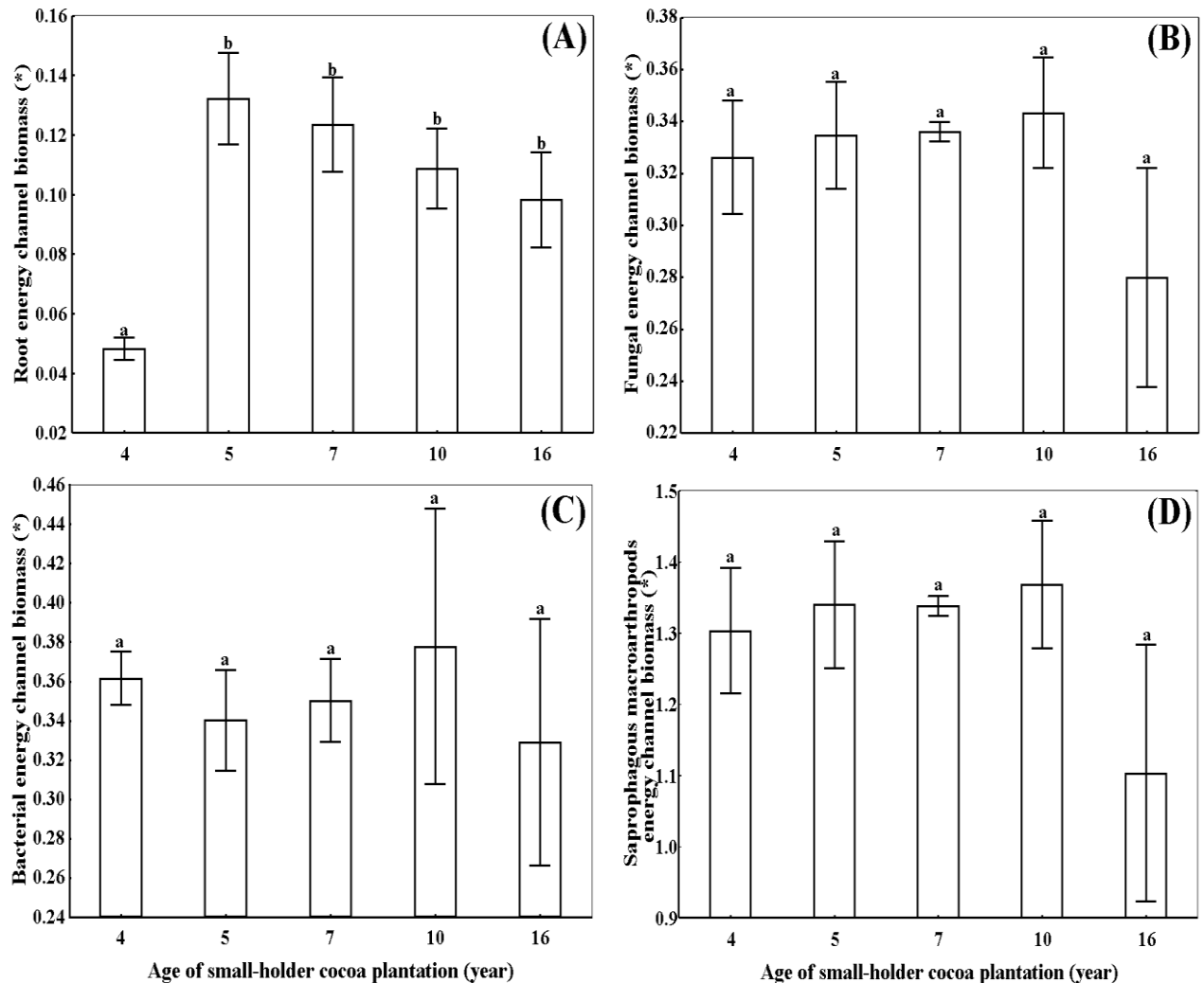


Figure 3. Standardised biomass (*) of (A) root energy channel, (B) fungal energy channel, (C) bacterial energy channel, and (D) saprophagous macro-arthropods energy channel in small-holder cocoa plantation aged 4, 5, 7, 10, and 16 years ($n = 20$, mean \pm standard error). Different letters placed above the bars indicate significant difference between ages of cocoa plantation at $p < 0.05$

Biomass in root energy channels in cocoa plantation aged 4 years was lower than that of cocoa plantation aged 5, 7, 10 and 16 years (Figure 3A). In this research, it was found that the pattern of changing biomass in root energy channels followed the pattern of changes in root biomass. A possible explanation on the pattern form biomass of root energy channels may be related to the dynamics of root defense mechanism against soil fauna feeding on root (Bonkowski *et al.*, 2009).

Biomass in energy channels of fungi, bacteria or saprophagous macro-arthropods between ages of cocoa plantation was not significantly different (Figure 3B, 3C, and 3D). This may be related to soil organic contents among cocoa plantations which were relatively similar (Table 2). Similarly, other indicators from changes of the structure of soil food webs which consisted on biomass ratio of fungal energy channels to bacterial energy channels and biomass ratio of saprophagous macro-arthropods energy channels to fungal energy channels between cocoa

plantation age were not significantly different (Figure 4C and 4D). In other words, the structuring in soil food web communities was influenced by combination of soil organic matter availability and biotic factors, such as facilitation, competition and predation..

Variation in energy channels indicated by the ratio of the organic fraction, the biomass ratio of fungi to bacteria, and the biomass ratio of energy channels was generally used to analyze changes in soil food web structure (Holtkamp *et al.*, 2008). The results showed that the ratio of

recalcitrant organic fraction to labile organic fraction, biomass ratio of fungi to bacteria, biomass ratio of fungal energy channels to bacterial energy channel (FB ratio), or the biomass ratio of saprophagous macro-arthropod energy channels to fungal energy channels between cocoa plantations were not significantly different (Figure 4A, 4B, 4C, and 4D). The proportion of recalcitrant organic fraction was slightly lower than labile organic fractions in all cocoa plantations (Figure 4A).

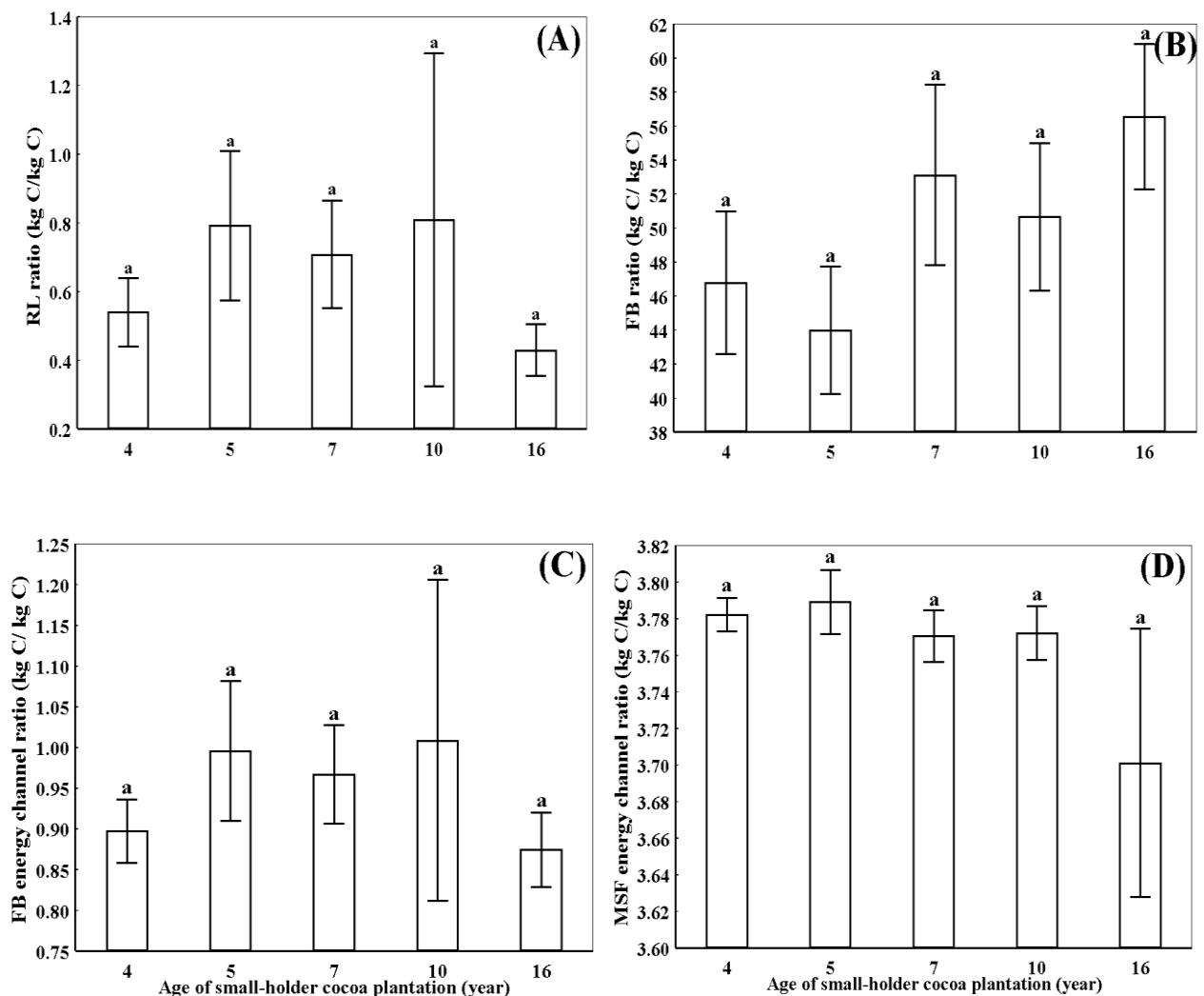


Figure 4. (A) ratio of recalcitrant organic fraction to labile organic fraction, (B) biomass ratio of fungi to bacteria, (C) biomass ratio of fungi energy channel to bacterial energy channel, and (D) biomass ratio of saprophagous macro-arthropods energy channel to fungal energy channel in small-holder cocoa plantation aged 4, 5, 7, 10, and 16 years. Values followed by the same letters placed above the bars indicate no significant difference between ages of cocoa plantation at $p > 0.05$

Fungal biomass was more dominant than the bacterial biomass in five different ages of cocoa plantation (Figure 4B). The dominance of fungal biomass in this study also reaffirms the opinion by Li and González (2008) that biomass of fungi was more dominant than biomass of bacteria in the tropical soil. Moore (1994) reviewed on some studies related soil food web in farm land and found that dominance of fungal biomass will be followed by the dominance of biomass in fungal energy channels. While in this study, although biomass of fungi was found most dominant (Figure 4B), but the biomass of fungal energy channels was lower than biomass of bacterial energy channels (Figure 4C). It is suspected by the presence of saprophagous macro-arthropods, earthworms, termites, and predators (ants, Coleoptera, and macro-Arachnids) potentially altering the distribution of biomass in fungal and bacterial energy channel in soil food webs micro-arthropods (Laakso, 1999; Mikola and Setälä, 1999; Wise, 2004; Wardle, 2006; Moya-Larano and Wise, 2007; Aira *et al.*, 2008).

CONCLUSION

Availability of soil organic matter as a source of primary energy for soil food web community in the small-holder cocoa plantation aged 4 to 16 years was relatively stable. Temporal changes in characteristics of soil food web structures were independent from net primary productivity in soil ecosystem. Variation in biomass at the trophic level 1, 2 or 3 and biomass in root energy channel of the soil food web is strongly influenced by biotic factors of macro-arthropods ground such as facilitation and recolonization capabilities and accessibility at different age of small-holder cocoa plantations.

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